



Tamm Review: Large-scale infrequent disturbances and their role in regenerating shade-intolerant tree species in Mesoamerican rainforests: Implications for sustainable forest management



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ABSTRACT

Forest management of tropical lowland and hill wet evergreen forests traditionally assumes that succession, species composition, and forest structure are largely driven by small, frequent disturbances. More recent ecological studies, archaeological findings, palynology and climate records demonstrate that tropical rainforests in general are not only subject to treefall disturbances but also to large-scale, infrequent disturbances driven by both past ancient and more recent human land use, and by natural forces of climate and geology. This paper reviews the case for the presence and extent of large-scale infrequent disturbances in Mesoamerica. We then use this knowledge to understand effects shaping species composition and structure. We evaluate current silvicultural regeneration systems for forest management based on the gap dynamics paradigm and propose potential alternative and complementary regeneration methods for forests and tree species that are driven by large-scale disturbances. We propose that the shade-intolerant timber species observed today are in large part a reflection of legacies of human land use and historical large-scale disturbances. Such species require larger, more dramatic disturbance regimes to regenerate and to attain the canopy in future managed forests. We suggest that such conditions are not provided for by current silvicultural systems within the region that require multiple entries to the stand every 15–30 years and should be coupled with liberation thinnings to promote shade-tolerant, commercially valuable timber species. Alternative silvicultural systems, such as shelterwoods and seed-tree methods of regeneration and management, purposefully promote the regeneration of valuable, shade-intolerant timber species. We propose applications for reserve design, and the management of non-timber forest products in conjunction with timber products to compliment such activities. These systems differ in their goals, species promoted (shade-tolerant vs. -intolerant) and the ecological assumptions driving their operations. We conclude that shelterwoods and seed-tree systems are more appropriate to manage forests rich in shade-intolerant timber species. Such methods need to be included in the suite of silvicultural options available to managers of tropical wet evergreen forests in Mesoamerica.

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1. Introduction

Philosophical approaches toward the management of tropical lowland and hill wet evergreen forests have traditionally relied on the assumption that succession, species composition, and forest structure is driven by gap dynamics. Much of this work was done toward the later part of the last century at a time when tropical forests were first being logged extensively for their timber (for example see gap dynamics work in Whitmore and Burnham, 1975; Hartshorn, 1978; Hartshorn, 1980; Brokaw, 1982; Brokaw, 1985; Brokaw, 1987; Denslow, 1980; Denslow, 1987; Whitmore, 1984; Brandani et al., 1988; Nuñez-Farfán and Dirzo, 1988; Hartshorn, 1989; Denslow et al., 1998). These ideas evolved from early ecological understandings of old-growth in temperate moist forests of Western Europe and North America (Clements, 1916; Sernander, 1936; Watt, 1947; Barden, 1980, 1981; Runkle, 1981).

The main driver of wet tropical forest dynamics in Mesoamerica (*i.e.* the geographical and cultural region from Mexico through to Panama) was thought to be single- and multiple-tree fall gaps driven by autogenic disturbance. Research on gap dynamics of neotropical rain forests is largely based on work carried out in Costa Rica and Panama from 1970 to 1990 (Hartshorn, 1980; Brokaw, 1982; Brokaw, 1985; Brokaw, 1987; Denslow, 1980; Denslow, 1987; Brandani et al., 1988; Nuñez-Farfán and Dirzo, 1988; Hartshorn, 1989; Denslow et al., 1998; Guariguata and Pinard, 1998).

Archaeological findings and climate records demonstrate that tropical rainforests are also subject to large-scale infrequent disturbances (LIDs) (Oliver, 1981; Attiwill, 1994; Dale et al., 1998; Foster et al., 1998; Sugden, 1992; Turner et al., 1997; Turner et al., 1998; Whitmore and Burslem, 1998; Burslem and Whitmore, 1999; Fredericksen and Putz, 2003; Mascorro et al., 2016). Examples of LIDs affecting tropical forests include hurricanes (Lugo et al., 1983; Basnet et al., 1992; Attiwill, 1994; Lugo and Scatena, 1996; Foster et al., 1998; Whitmore and Burslem, 1998; Chazdon 2003); convective windstorms (Ediriweera et al., 2008); severe droughts (Condit et al., 1995; Potts, 2003; Engelbrecht et al., 2007); fires (Kauffman, 1991; Cochran et al., 1999; Urquhart, 2008); floods (Gullison et al., 1996; Foster et al., 1998); volcanic eruptions; and landslides following periods of heavy rains or seismic activity (Garwood et al., 1979; Guariguata, 1990; Foster et al., 1998; Sigl et al., 2015). In addition, evidence suggests that human influence from ancient permanent agricultural systems, swidden cultivation, and the management of fallow

fields played an important role in the origin of many rain forests (Deevey et al., 1979; Gómez-Pompa, 1987; Leyden, 1987; Denevan, 1992; Bush and Colinvaux, 1994; Peters, 2000; Cooke, 2005; Nichols, 2015).

In the case of certain kinds of disturbances such as hurricanes, floods, fires, earthquakes, permanent agricultural systems, and volcanic activity, the forces exerted may change the landscape dramatically (Garwood et al., 1979; Lugo and Scatena, 1996; Everham and Brokaw, 1996; Turner et al., 1997; Foster et al., 1998; Michener and Hauber, 1998). Milder events such as droughts, groundstory fires, swidden cultivation and winds, although capable of rearranging vegetation are not generally catastrophic (Attiwill, 1994; Condit et al., 1995; Everham and Brokaw, 1996; Lugo and Scatena, 1996; Chazdon, 2003; Baker et al. 2008). Both kinds of events are a major episodic component of the disturbance regime complimenting the continuous smaller single- and multiple-tree fall disturbances that were thought to be the main driver of species composition and structure.

A large body of scientific inquiry has led a paradigm shift away from considering tropical forests as stable tree communities. Tropical forest ecologists increasingly recognize the dynamic nature of forests and the influence of large-scale episodic disturbances occurring over long intervals of time (Oliver, 1981; Brandani et al., 1988; Sprugel, 1991; Brown and Whitmore, 1992; Attiwill, 1994; Lugo and Scatena, 1996; Clark, 1996; Whitmore and Burslem, 1998; Dale et al., 1998; Foster et al., 1998; Turner et al., 1997; Turner et al., 1998; Chazdon, 2003; Fredericksen and Putz, 2003; Baker et al., 2005). Current tropical forest management paradigms, however, do not reflect the state-of-the-art ecological understanding of tropical forest dynamics.

In this paper we review the case for the presence and extent of LIDs in Mesoamerican wet evergreen rainforest. We then use this knowledge to understand the successional forces shaping species composition and structure. We evaluate current silvicultural regeneration methods for forest management and propose potential alternative and complementary regeneration methods for forests and tree species adapted to LIDs. The paper is organized into four sections comprising: (1) a description of the physical environment defining rainforests in Mesoamerica; (2) a review of the evidence that supports the role LIDs play in Mesoamerican rain forests (both human-induced and natural); (3) a review of current methods of forest management and logging (*i.e.* based on minimum felling diameter); and lastly (4) a case for the inclusion and application of shelterwoods and seed-tree systems for regenerat-

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